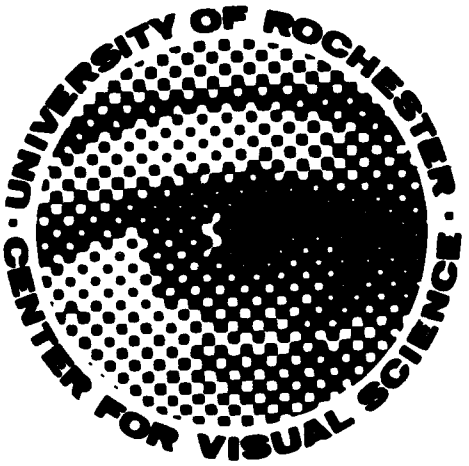
NEW INSIGHTS ON VISUAL CORTEX

ABSTRACTS

Sixteenth Symposium
June 16-18, 1988



UNIVERSITY OF ROCHESTER

CENTER FOR VISUAL SCIENCE

19 AUG 1988

UNCLASSIFIED
SECURITY CLASSIFICATION OF THIS PAGE

REPORT DOCUMENTATION PAGE

1a. REPORT SECURITY CLASSIFICATION	1b. RESTRICTIVE MARKINGS
2a. SECURITY CLASSIFICATION AUTHORITY	3. DISTRIBUTION / AVAILABILITY OF REPORT Approved for public release; distribution unlimited.
2b. DECLASSIFICATION / DOWNGRADING SCHEDULE	
4. PERFORMING ORGANIZATION REPORT NUMBER(S)	5. MONITORING ORGANIZATION REPORT NUMBER(S) AFOSR.TR. 88 0983
6a. NAME OF PERFORMING ORGANIZATION: University of Rochester 6b. OFFICE SYMBOL (If applicable):	7a. NAME OF MONITORING ORGANIZATION: AFOSR/NL
6c. ADDRESS (City, State, and ZIP Code): Center for Visual Science 274 Meliora Hall, River Campus Rochester, NY 14627	7b. ADDRESS (City, State, and ZIP Code): Bldg. 410 Bolling AFB, DC 20332-6448
8a. NAME OF FUNDING / SPONSORING ORGANIZATION: AFOSR 8b. OFFICE SYMBOL (If applicable): NL	9. PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER: AFOSR-88-0170
8c. ADDRESS (City, State, and ZIP Code): Bldg 410 Bolling AFB, DC 20332-6448	10. SOURCE OF FUNDING NUMBERS PROGRAM ELEMENT NO: 61102F PROJECT NO.: 2313 TASK NO: A5 WORK UNIT ACCESSION NO:

11. TITLE (Include Security Classification)

New Insights on Visual Cortex

12. PERSONAL AUTHOR(S)
Walter Makous, John Maunsell, Tatiana Pasternak

13a. TYPE OF REPORT	13b. TIME COVERED	14. DATE OF REPORT (Year, Month, Day)	15. PAGE COUNT
Final	FROM 15 May 88 TO 14 May 89	June 88	29

16. SUPPLEMENTARY NOTATION

17 COSATI CODES			18. SUBJECT TERMS (Continue on reverse if necessary and identify by block number)
FIELD	GROUP	SUB-GROUP	

19. ABSTRACT (Continue on reverse if necessary and identify by block number)

This is a record of the sixteenth symposium sponsored by the Center for Visual Science at the University of Rochester on June 15-18, 1988. It consists of abstracts from the papers presented at the meeting and a list of the participants. Five topical sessions each included four papers. The sessions were: early visual processing, parallel channels cortical processing (approaches), levels of cortical processing, and visuomotor integration

2

20. DISTRIBUTION / AVAILABILITY OF ABSTRACT ☐ UNCLASSIFIED/UNLIMITED ☐ SAME AS RPT ☐ DTIC USERS	21. ABSTRACT SECURITY CLASSIFICATION
22a. NAME OF RESPONSIBLE INDIVIDUAL: Dr. John Tangney	22b. TELEPHONE (Include Area Code): (202) 767-5021 22c. OFFICE SYMBOL: NL

DD FORM 1473, 84 MAR — 83 APR edition may be used until exhausted. All other editions are obsolete.

SECURITY CLASSIFICATION OF THIS PAGE
UNCLASSIFIED

88 10 5 215

NEW INSIGHTS ON VISUAL CORTEX

ORGANIZING COMMITTEE

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PREFACE

This is a record of the sixteenth symposium sponsored by the Center for Visual Science at the University of Rochester on June 15-18, 1988. It consists of abstracts from the papers presented at the meeting and a list of the participants.

We thank the speakers for their interesting and informative presentations, and we also thank the members of CVS who helped with the meeting, particularly Julie Deister and Teresa Williams, who adroitly handled most of the administrative duties and responsibilities of the meeting. Primary financial support of the meeting was provided by a contract with the Life Sciences division of the Air Force Office of Scientific Research, with assistance from a Center Grant (EY01319) awarded to the Center for Visual Science by the National Eye Institute.

TABLE OF CONTENTS

LEVELS OF PROCESSING IN VISUAL CORTEX

VISUOMOTOR INTEGRATION

EARLY PROCESSING

ROBERT SHAPLEY	"P and M Pathways in the Primate Visual System"
DAVID MASTRONARDE	"Retinal X and Y Input to the Cat LGN Diverges into Classes of Cells with Different Spatial or Temporal Properties"
MURRAY SHERMAN	"Functional Organization of the Cat's Lateral Geniculate Nucleus"
JOHN ROBSON	"Linear and Nonlinear Behavior of Neurons in the Visual Cortex of the Cat"

P and M Pathways in the Primate Visual System

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Two parallel signal paths exist between retina and visual cortex in macaque monkeys. The P retinal ganglion cells project to Parvocellular layers in LGN, and then Parvocellular neurons connect to cortical cells in layer IVcβ in V1 cortex. The M ganglion cells drive Magnocellular geniculate neurons which then drive cortical cells in layer IVcα of V1. The responses of M and Magnocellular cells are large at low luminance contrast and saturate to optimal stimuli at about 10-20% contrast. The responses of P cells and their Parvocellular targets are small at low contrast and grow proportionally to contrast up to 60% contrast. When mean retinal illuminance is reduced to 1 Td or less, the response to a fixed contrast declines, for both cell types, so that P and Parvocellular cells become inexcitable by visual patterns. In this situation, Magnocellular input to the cortex is favored. Parvocellular input to cortex is favored when color-contrasting patterns near isoluminance are used because Magnocellular neurons (and their M inputs) are poorly responsive to color-exchange near isoluminance. Between individuals the isoluminant point varies but within an individual the Magnocellular neurons' responses go to zero at about the same isoluminant balance.

Retinal X and Y Input to the Cat LGN Diverges into Classes of Cells with Different Spatial or Temporal Properties

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The A layers of the lateral geniculate nucleus (LGN) of the cat receive input from retinal axons of two classes, X and Y, and project to primary visual cortex. To a first approximation, the LGN can be thought of primarily as relaying two parallel streams of X and Y information to cortex. However, under this view, it is a mystery why the A layers contain over five times as many cells as retinal X and Y axons. Experiments that involve directly recording from the inputs to individual LGN cells have provided a more detailed view of the variety of cells in the LGN. Cross-correlation techniques are used to assess whether a particular ganglion cell provides excitatory, inhibitory, or no input to an LGN cell. Relay cells with a variety of spatial properties are generated by varying the number and type of convergent excitatory inputs. The series of cells consists of single-input X-cells (X_S) with the receptive-field center size and spatial resolution of single retinal X-cells, multiple-input X-cells (X_M) and mixed-input (X/Y) cells with center size and spatial resolution intermediate between those of retinal X- and Y-cells, predominantly single-input Y-cells with center size about the same as single retinal Y-cells, and multiple-input Y-cells with larger centers and lower resolution than retinal Y-cells. These cells all have fast and relatively transient responses to visual stimuli; there are also relay cells with very different temporal properties that receive a particular pattern of inhibitory input. These "lagged" cells have delayed and relatively sustained responses; almost all of these cells are X-type, with the spatial resolution of single retinal X-cells, but there is some evidence for lagged Y-cells as well. Cells that do not project to visual cortex presumably provide inhibitory functions within the LGN; again, most of these cells are X-type but there is some evidence for Y-interneurons as well. Quantitative analysis indicates that these various kinds of cells fall into distinct cell classes, except for the single- and multiple-input Y-cells. Thus, the two retinal X and Y streams branch in the LGN into multiple pathways with potentially distinct functional roles.

Functional Organization of the Cat's Lateral Geniculate Nucleus

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The component X and Y cells of the A-laminae of the cat's lateral geniculate nucleus represent the main relay between retina and visual cortex. These two cell classes are integral links in two parallel and largely independent retino-geniculo- cortical streams known as the X and Y pathways. Both in retina and the lateral geniculate nucleus, X and Y cells differ in many morphological and physiological features, including receptive field properties. The observation that the receptive fields of geniculate X or Y cells are virtually identical to those of their retinal X or Y afferents creates the misimpression that the lateral geniculate nucleus represents a simple relay. However, geniculate relay cells receive only 10-20% of their synaptic inputs from retina. The other inputs derive chiefly from visual cortex, from local GABAergic neurons (interneurons and cells of the nearby perigeniculate nucleus), and from the brainstem reticular formation. The last are represented mostly by cholinergic inputs from the parabrachial region, but also by noradrenergic inputs from the locus coeruleus and serotonergic inputs from the raphe nucleus. These nonretinal inputs do not dramatically alter receptive field features per se, but instead seem to control excitability of the relay cells and thus gate or control the gain of retino-geniculo-cortical transmission. This gating function, which may be an important neural substrate for various forms of visual attention, is quite different from the function of circuitry elsewhere in the visual system (e.g., the retina and visual cortex), where the elaboration of receptive field properties seems to be the primary task. We have thus tried to analyze geniculate circuits with a variety of physiological and morphological techniques. The details of these circuits, correlates between morphological and physiological data for the relay cells, and interesting differences between these patterns for the X and Y pathways will be discussed.

Linear and Non-Linear Behavior of Neurones in the Visual Cortex of the Cat

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When tested with spatially-localized stimuli, neurons in the primary visual cortex of the cat respond only when the stimulus is located within some restricted region of the visual field. When tested with extended gratings, these same neurons respond only when the 2-dimensional spatial frequency of the stimulus falls within some restricted range. This stimulus selectivity in both space and spatial frequency may be explained by assuming that the response of a cortical cell is determined by the linear weighted sum of signals arising in different locations within the cell's receptive field or, in the case of complex cells, within subunits of the receptive field. With this assumption, the characteristic selectivity of most cortical cells can be explained by a 2-dimensional spatial weighting function with an appropriate number of adjacent elongated regions of alternating sign. It must be noted, however, that non-linear action may result in the spatial weighting function of individual cells being somewhat incorrectly estimated from the usual experimental observations.

Since the responsive area of each cortical cell is restricted in two dimensions not only of space but also of spatial frequency, the visual image occupying any particular patch of the visual field can only be represented in the cortex by the activity of a substantial number of cells having co-extensive or overlapping spatial receptive fields. While this does not of itself explain why there should be such a very large number of cells in the visual cortex, it suggests that we should look for an explanation of this very large number in the existence of multiple overlapping transforms, each corresponding to a differently located image patch of a certain size. Moreover, insofar as there exist sets of cells having spatially co-extensive receptive fields whose spectral receptive fields together provide a complete coverage of 2-D spatial frequency, we may reasonably suppose the visual image to be represented in the cortex by multiple patch-by-patch spatial-frequency transforms.

However, it has been suggested that the above notions are invalidated by the non-linearities of cortical-cell characteristics. In particular the non-linearities manifested in response rectification, response saturation and cross- orientation inhibition seem to be inconsistent with any simple idea of spatial-frequency representation in the cortex. Even if it is accepted that response rectification may be of little consequence if cortical cells, like on-center and off-center retinal ganglion cells, exist in pairs of opposite polarity, the other effects do, at first sight, seem to raise more serious objections. It can be argued, however, from the nature of these effects (1), that both response saturation and cross-orientation inhibition are simply manifestations (in an experimental situation) of a cortical mechanism intended to make the cortical representation as independent as possible of extraneous factors which result in the local contrast of the visual image being multiplicatively scaled.

Such a contrast-normalizing mechanism would be a desirable feature of a system designed to analyze images of the natural world.

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(1) Observations to be reported were made in R. D. Freeman's laboratory in collaboration with RDF and Izumi Ohzawa.

PARALLEL CHANNELS

DAVID VAN ESSEN	"Information Processing Strategies in Primate Visual Cortex"
JOSEPH MALPELI	"Cortical Responses Revealed by Reversible Inactivation"
WILLIAM MERIGAN	"Visual Capacities of P and M Pathways"
PATRICK CAVANAGH	" What Low-Level Vision Tells High-Level Vision

Information Processing Strategies in Primate Visual Cortex

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Visual cortex in the macaque monkey consists of more than two dozen distinct visual areas. These can be arranged in an anatomically-defined hierarchy involving at least ten processing stages. Anatomical and physiological evidence suggests the presence of a small number of processing streams coursing through successive stages of this hierarchy. However, there is considerable convergence and divergence among these streams. This may be related to the multiplicity of computational strategies that allow each low-level sensory cue (e.g., velocity) to contribute to many distinct aspects of perception (e.g., motion, depth, and form). Some of these computational strategies may involve dynamic control over the way in which information is routed through visual cortex.

Cortical Responses Revealed by Reversible Inactivation

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We have studied the contributions of individual geniculate layers to cortical function by reversibly inactivating segments of layers while assessing visually evoked activity in cortex. In cat area 17, dependence upon the A layers of the lateral geniculate nucleus is most common and profound for the cortical layers receiving direct A-layer inputs: layers 4 and 6, and in particular for simple cells in these layers (Malpeli *et al.*, *J. Neurophysiol.* **56**: 1062, 1986). In contrast, few if any cells in area 17 depend upon inputs from the C layers or the medial interlaminar nucleus. We have extended these experiments to prestriate cortex, examining geniculate contributions to activity in the PMLS region of lateral suprasylvian cortex and in area 18 supragranular layers.

Inputs to area 18 from the A layers and layer C are comparable in magnitude and extend into the supragranular layers. The effects of geniculate inactivations on simple cells mirrored the vertical distribution of geniculate inputs, being greatest in the lower half of layer 3. Simple cells, which are frequently encountered in the supragranular layers, tended to be dominated either by A- or C-layer inputs. As in area 17, supragranular complex cells were much less dependent upon single geniculate subdivisions than were simple cells, although the difference between simple and complex cells in this regard was not nearly as striking as in area 17.

Although the PMLS region receives little or no direct inputs from the A layers, inactivation of layer A had considerably greater effects on activity than inactivation of the C-layers or the medial interlaminar nucleus. Dependence on layer A was most evident in patches receiving associational inputs from area 18. Area-18 cells identified as projecting to PMLS cortex by means of antidromic activation were all simple cells dominated either by layer A or by the C-layers. On average their dependence on layer A matched that of cells in PMLS cortex within patches receiving area 18 input.

In conclusion, the laminar organization of the lateral geniculate nucleus is reflected in activity across several areas of visual cortex, involving associational as well as direct connections. Simple cells are important conduits of individual parallel inputs, in associational as well as intrinsic circuits.

Visual Capacities of the P and M Pathways

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Physiological responses of neurons in P and M pathways have been compared for contrast sensitivity, spatial and temporal resolution, chromatic sensitivity, and low luminance contrast detection. In general, neurons in the two pathways were found to be similar in spatial resolution, those in the M pathway superior in temporal resolution as well as high and low luminance contrast sensitivity, and those in the P pathway superior in chromatic sensitivity.

Our psychophysical studies give an independent picture of the visual capacities of these two pathways. We have measured visual thresholds in monkeys with damage to either the P or M systems. We find that the P pathway plays a dominant role in the color vision of the primate, and the M pathway in sensitivity at high temporal frequencies. On the other hand, our results indicate that the P pathway is the major contributor to detection of low contrasts, especially at low temporal frequencies. We also find, as was suggested by its high sampling density, that the P pathway dominates detection at high spatial frequencies.

These results indicate some segregation of function between P and M pathways, and, thus, suggest some limits on the possible roles of these pathways in visual processing.

What Low-Level Vision Tells High-Level Vision

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An image can be considered a superposition of several surface attributes, and in the first area of visual cortex, cells respond to many of these attributes conjointly. We have examined the coding of 2-D shape for five different attributes (color, texture, motion, binocular disparity, and luminance) and evaluated whether these codes are analyzed independently for each attribute.

Physiological studies have shown that orientation and size coding is available in area V1 for stimuli defined by luminance. To identify whether orientation codes are available for the other attributes as well, we first measured tilt aftereffects with grating stimuli defined by each of five attributes. A tilt aftereffect of about the same magnitude was found for each stimulus type. Although these data suggest that a similar analysis of orientation may be performed for each attribute, they do not specify whether this analysis occurs independently for each. To test for independence, we used an opposing aftereffects paradigm. For example, observers adapted to a grating defined by luminance that tilted to the left alternating with a second grating defined by color that tilted to the right. The tilt aftereffect, measured on vertical tests defined by color or by luminance in this case, showed that direction of the tilt aftereffect was contingent on *whether* the test was defined by color or luminance. These results indicated similar, independent analyses of orientation for these two attributes. However, independence was not found between stimuli defined by motion, texture or binocular disparity, implying that orientation analyses for these three attributes may occur at a single site. Finally, using the size aftereffect paradigm, we were also able to induce simultaneous and opposite size aftereffects for color and luminance stimuli. Overall, these data suggest that there are at least three functionally independent analyses: one for luminance; one for color (actually two, one for each of two color axes); and a common one for motion, stereo and texture.

Why should these 2-D, size and orientation analyses be duplicated in several pathways? Certainly, reliability is increased by duplicating the analysis across attributes and this is especially true in the case of color and texture contours since these are more reliably linked to object borders than is luminance (luminance contours are often confounded by extraneous shadow borders). In addition, if we allow that the analysis of the visual image proceeds in parallel in different pathways, the size and orientation codes may be common to all of them so that the results can be subsequently compared or recombined using a common description. In one sense then, size and orientation codes may be part of an internal standard for image definition in the visual system. Why specifically size and orientation? Both contour representations (e.g. recognition-by-components) and invariant 2-D shape codes are well served by size and orientation information. Difficulties in parsing image contours suggest that initial memory access may be based not on contour representations, however, but on 2-D image codes.

CORTICAL PROCESSING: NEW APPROACHES

CHARLES GILBERT	"Horizontal Integration in the Visual Cortex"
GARY BLASDEL	"Using Optical Dyes to Visualize Cortical Activity"
LANCE OPTICAN	"Temporal Codes and Spatial Messages in the Visual System"
TERRENCE SEJNOWSKI	"Network Model of Shape-From-Shading: Neural Function Arises From Both Receptive and Project Fields"

Horizontal Integration in the Visual Cortex

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A common pattern of intrinsic cortical connections and of connections between different cortical areas is their widespread and patchy distribution. An individual pyramidal cell can project for many millimeters within its resident area, covering an area of cortex that is likely to represent a greater visual field area than that covered by the cell's own receptive field. The axon collaterals of such a cell are distributed in discrete clusters, spaced approximately 1 mm apart. One can also visualize the long range clustered horizontal projections by using extracellular retrograde tracers, which show that clusters of cells covering a large area (up to 8 mm in diameter) project to the injection site. When mapped onto a plane parallel to the cortical surface, the cell clusters are seen as systems of branching bands, reminiscent of the orientation and ocular dominance columns. To determine the relationship between the clustering pattern and the orientation columns, we have used two approaches: cross-correlation analysis and combining retrograde labeling of intrinsic and cortico-cortical projections with labeling of orientation columns by 2-deoxyglucose autoradiography.

In the monkey striate cortex, cross-correlation analysis confirmed the segregation of connections between the cytochrome oxidase blob system and the interblobs. This approach showed an even greater degree of specificity than was shown with earlier anatomical studies, with interblob interactions between cells of similar orientation specificity, and blob interactions between cells of similar receptive type and color opponency. These specificities were then confirmed by typing the blobs with multiple electrode penetrations and examining the connectivity between blobs with HRP transport. The cross-correlation technique also presents evidence for a degree of interaction between the color and form system. Color oriented cells, for example, which tend to have a "peri-blob" distribution, have interactions with color-specific unoriented cells within the blobs.

The specificity of the horizontal connections for orientation columns of matched orientation preference has also been demonstrated in the cat by injecting a single orientation column with rhodamine filled latex microspheres (beads), which labels cells projecting to the injection site, followed by labeling of vertical orientation columns by 2-deoxyglucose autoradiography. When the injection was placed in a vertical orientation column, the clusters of retrogradely labeled cells lay over vertical orientation columns. Another set of experiments showed that the projection from area 17 to area 18 followed a similar rule, with vertical orientation columns in 17 projecting to vertical columns in 18, and horizontal to horizontal. Taken together, our findings indicate that horizontal connections relate columns of like functional specificity. The intrinsic and cortico-cortical projections form a repeating pattern of widely divergent connections that allow integration over progressively larger parts of the visual field. The functional consequences of this pattern of connectivity may be the construction of larger receptive fields and a sensitivity to context in the visual environment.

Studies of Motion Selectivity to Visual Stimuli With and Without Oriented Contours in Monkey Striate Cortex Using Optical Techniques

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We used optical techniques based on video imaging technology and the voltage sensitive dye NK2367 to analyze the functional anatomy of motion selectivity to visual stimuli with and without oriented contours in monkey striate cortex (*Macaca nemestrina*). Previous work using this approach (Blasdel and Salama, *Nature* 1986) revealed a close relationship between the continuity of orientation mapping and the centers of ocular dominance columns: orientation shifts most continuously in patches of cortex that lie between O.D. column centers. Further analysis of this organization reveals that regions of greatest orientation continuity coincide with regions displaying the greatest selectivity for orientation. Since the boundaries of these regions, where orientation selectivity is much weaker, lie at the centers of ocular dominance columns, they include cytochrome oxidase blobs, the cells of which have been shown previously (Livingstone and Hubel, 1984) to lack orientation selectivity.

We compared the patterns of activity generated by visual stimuli with and without oriented contours by using one pattern that consisted of a multi-frequency, square wave grating, similar to those that had been used previously to study the mapping of orientation selectivity (Blasdel and Salama, 1986), and another that consisted of a field of random white dots (2% density with each dot subtending 0.1 degree of visual angle). Both patterns moved uniformly in the same direction. The results of this comparison revealed a surprising and robust difference in the direction of preferred movement for each of the two patterns. Maps of orientation/movement selectivity generated by the moving multifrequency square wave grating (oriented perpendicular to the direction of motion) differed, in most parts of the cortex, from those generated by the field of random dots by an angle of approximately 90 degrees. In places where the motion selectivities for these two stimuli did not differ by 90 degrees, they tended to be parallel. Moreover, there appears to be a strong correlation between regions where the motion selectivities for visual stimuli with and without oriented contours are orthogonal, and the patches noted above, where cells are most tightly tuned for orientation, and where the orientational preference of neighboring cells changes most continuously.

Temporal Codes and Spatial Messages in the Visual System

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How are pictures represented within the brain? We have shown that individual neurons use a multidimensional temporal code to convey information about multiple stimulus features simultaneously without confounding them. By modelling each neuron as a collection of nonlinear spatial-to-temporal filters whose outputs are multiplexed into the response, i.e., the spike train, we can accurately predict the responses of both LGN neurons and complex neurons of striate cortex to arbitrary pictures. When the multidimensional responses are decomposed and viewed in a 3-dimensional (stereo) graphic display, the neuronal responses to each stimulus pattern lie near a uniquely oriented plane. Other stimulus features, e.g., duration and luminance, determine the response's position on that plane. These constraints are evidence for an intrinsic neuronal code, which can be interpreted in terms of visual features. Our findings imply a new interpretation for the functional roles of single neurons. Each neuron conveys a multidimensional, but low resolution, description of the stimulus in temporally modulated messages that are multiplexed onto the spike train. The messages are encoding the visual properties of the stimulus, and must be considered as filtered representations and not abstractions. Such multiple messages require fewer cells to encode information, make decoding relatively simple by preventing feature confounding, form a code independent of synaptic scaling, and provide a way to index information about particular features processed in different parts of the brain.

Network Model of Shape-from-Shading: Neural Function Arises from Both Receptive and Projective Fields

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The visual system can extract information about the shape of a 3-D object from the continuous gradations of light and dark found on its shaded surface. To investigate the computation of shape from shading, a learning algorithm was used to construct a neural network model which determines surface curvatures from images of simple geometrical surfaces. Receptive fields developed by units in the network were surprisingly similar to those of neurons observed in visual cortex. These neurons are commonly interpreted as "edge" or "bar" detectors, but have never previously been associated with shading. This network illustrates the difficulty of trying to deduce neuronal function solely from receptive fields. Also important are the connections a neuron makes with neurons in subsequent stages of processing, which is called its "projective field."

LEVELS OF PROCESSING IN VISUAL CORTEX

PETER LENNIE	"Chromatic Signals in Cortex"
ALAN COWEY	"Cells and Pathways Underlying 'Blindsight'"
WILLIAM NEWSOME	"Psychophysics and Physiology of a Perception Decision"
EDMUND ROLLS	"Information Processing in the Inferior Temporal Visual Cortical Areas of the Macaque"

Chromatic Signals in Cortex

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Psychophysical experiments give rise to clear expectations about the physiology of the first stage of color vision (receptors) and the second stage (the red-green and yellow-blue opponent mechanisms and the achromatic mechanism). We now know that the second stage inferred from psychophysical experiments is actually a third (or perhaps further) stage in the physiological elaboration of signals and does not arise until at least striate cortex. The intervening ganglion cells and parvocellular neurons in l.g.n., because they are linear, are transparent to psychological investigation.

Neurons in striate cortex transform substantially the signal received from l.g.n., but do not fall neatly into the classes inferred from psychophysical observations. The overt chromatic opponency so common in the l.g.n. is relatively uncommon in cortical neurons: most simple and complex cells prefer nearly achromatic stimuli, and most appear to be driven predominantly by a signal from the long-wavelength sensitive cones. Overt color opponency is most common in neurons with concentrically organized receptive fields; these neurons, which are most common in parts of layer IV and in layer VI, prefer chromaticities that are bimodally distributed, but the bimodality is less sharp than in l.g.n. With rare and striking exceptions, neurons in striate cortex are no more sharply tuned for chromaticity than are neurons in l.g.n. The chromatic signatures of neurons, which provide clues about the transformation of l.g.n. signals, suggest that striate cortex is an early stage in the elaboration of chromatic signals.

Cells and Pathways Underlying "Blindsight"

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After part of the striate cortex is damaged, ganglion cells die in the corresponding part of the retina, in people as well as in monkeys. This transneuronal degeneration proceeds over several years. In order to quantify the overall loss after many years, we (Cowey, Stoerig and Perry) counted ganglion cells in the Nissl-stained flat-mounted retinae of macaque monkeys whose left striate cortex had been completely removed eight years earlier. The transneuronally degenerated hemiretina was compared with the normal hemiretina and with similarly prepared retinae from normal monkeys. About 80% of the retinal ganglion cells had disappeared in the central 20 degrees of the degenerated hemiretina. At greater eccentricities about 50% had died and the degeneration was present right to the edge of the retina. In order to determine which cell classes are involved, and the extent to which they are involved, surviving ganglion cells were morphologically classified in the other eye, which had been labelled from its optic nerve with horseradish peroxidase. Measurements of soma size and dendritic field size of morphologically classified cells in the degenerated part of the retina showed that they are normal for their particular class. However, in comparison with the intact hemiretina the overall mean soma size of labelled ganglion cells in the degenerated hemiretina was abnormally large, suggesting that it is the smaller cells that have died. Classification of labelled survivors shows that the population of Pβ cells is reduced by up to 85% whereas there is no discernible change in the number of Pα and Pγ cells, whose proportion therefore increases. The residual visual abilities that survive ablation of striate cortex in primates, often referred to as "blindsight" are therefore achieved without the great majority of the commonest retinal ganglion cells, most of which are color opponent. If the remaining Pβ ganglion cells contribute to residual vision, the characteristics of the latter should show marked variation with small changes in the position of the retinal image, given that the anatomical coverage factor for surviving Pβ cells is now less than unity. By injecting an anterograde tracer into the eye and a retrograde tracer into extrastriate cortex it can be shown that at least some of the surviving Pβ cells and the intact population of Pα cells project to isolated surviving projection neurons in the otherwise degenerated dorsal lateral geniculate nucleus. These geniculate cells project in turn to extrastriate visual cortex, notably to visual area V4. Whether the direct retino-geniculo-extrastriate pathway is intact in patients with 'blindsight' and, if so, why it can not mediate visual experiences, remains mysterious.

Psychophysics and Physiology of a Perceptual Decision

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Studies from a number of laboratories have identified a pathway in primate visual cortex that appears to be devoted to the analysis of visual motion information. It is our goal to determine the ways in which neural activity within this pathway contributes to specific perceptual phenomena. Our approach involves complementary psychophysical and physiological investigations of motion perception in awake, behaving monkeys. For both psychophysical and physiological experiments, we employ a dynamic random dot stimulus in which the experimenter may systematically vary the intensity of a motion signal that is spatially interspersed amongst random motion noise. We have characterized perceptual responses to this stimulus by measuring the threshold intensities for which monkeys can successfully perform direction discriminations in a two-alternative, forced-choice paradigm. In addition, we have made chemical lesions of an identified component of the cortical motion pathway (extrastriate visual area MT) to demonstrate that neural activity in this area selectively contributes to the perception of motion in these stimuli.

In recent physiological experiments, we have used the same random dot stimuli to measure the threshold intensities at which single direction selective neurons in MT provide reliable information about direction of motion. We derived a "neurometric function" for each neuron using methods based on signal detection theory, and we calculated a "psychometric function" for the monkey's perceptual performance on the same set of trials. The stimulus location and direction of motion were optimized for the neuron being studied. For most MT neurons, both the absolute threshold and slope of the neurometric function were comparable to those of the psychometric function. Furthermore, a preliminary analysis indicates that trail-to-trail fluctuations in psychophysical performance near threshold are associated with statistical fluctuations in the responses of single MT cells. These observations suggest that MT neurons may contribute directly to perceptual decisions concerning visual motion.

The Representation of Information in the Temporal Lobe Visual Cortical Areas of Macaque Monkeys

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The ways in which information is represented, processed, and stored in the temporal lobe of primates as shown by recordings from single neurons in alert macaque monkeys are considered.

1) There is specialization of function in different temporal cortical areas concerned with vision. For example, areas TPO, PGa and IPa are multimodal; the inferior temporal gyrus and adjacent areas (TE3, TE2, TE1, TEa and TEm) are primarily unimodal visual areas; areas in the cortex in the anterior and dorsal part of the superior temporal sulcus (e.g., TPO, IPa and IPg) have neurons specialized for the analysis of moving visual stimuli; and neurons responsive primarily to faces are found predominantly in areas TPO, TEa and TEm. Thus neuronal response properties are different in different architectural subdivisions of the temporal lobe cortex (Baylis, Rolls, & Leonard, 1987).

2) Within areas, individual stimuli, objects, or responses are coded as the pattern of firing across a subpopulation of neurons. That is, ensemble encoding rather than "grandmother cell" encoding is used. Evidence for this comes from recordings made in temporal visual cortical areas involved in face recognition (Baylis, Rolls, & Leonard, 1985).

3) It is argued that this type of tuning found is a delicate compromise between very fine tuning, which has the advantage of low interference in neuronal network operations but the disadvantage of losing the emergent properties of storage in neuronal networks, and broad tuning, which has the advantage of allowing the emergent properties of neuronal networks to be realized but of leading to interference between the different memories stored in the network (Rolls, 1987).

4) Neurons in these visual cortical areas are seen as filters, which as an ensemble give a unique representation of a stimulus in the environment, and preliminary evidence that the responses of some of these neurons are altered by experience so that new stimuli become incorporated in the network is presented. For example, 6/22 neurons tested showed significant alterations in the magnitude of the response to the different members of a set of novel faces in the first few presentations of the faces. These alterations in the degree to which the neurons responded to different faces took place during the first few presentations, and a similar effect was not found during repeated presentations of familiar faces. The role of competition in the function of such networks is considered.

5) It is found that the representation which is built in temporal visual cortical areas shows considerable invariance with respect to changes of for example size, contrast (Rolls and Baylis, 1986) and spatial frequency (Rolls, Baylis and Leonard, 1985; Rolls, Baylis, & Hasselmo, 1987). The fact that the responses of these neurons show considerable invariance over changes in size we take as evidence that the encoding is not in retinal coordinates. Alternatives are that it is in viewer-centered or object-centered coordinates.

6) There are several findings which indicate that one of the representations of visual information built by some neurons is object-centered rather than viewer-centered (Hasselmo, Rolls, Baylis, & Nalwa, 1989). For example, we utilized the fact that some neurons with responses selective for faces respond only if the face is moving (Perrett *et al.*, 1985) to investigate whether the encoding of faces by these neurons is in viewer-centered or object-centered coordinates. For 10 neurons we showed that the neuron responded to particular movements which could only be described in object-centered coordinates. For example, four neurons responded vigorously to a head undergoing ventral flexion, irrespective of whether the head was viewed full face, to either profile, or even from the back of the head. These different views could only be specified as equivalent in object-centered coordinates. Five different neurons had responses only to a head undergoing dorsal flexion. Further, the movement specificity was maintained across inversion, responding for example to ventral flexion of the head irrespective of

whether the head was upright or inverted for all four of these neurons tested. In this procedure, retinally encoded or viewer-centered movement vectors are reversed, but the object-centered description remains the same. It was of interest that 3 of these neurons generalized across different heads performing the same movements.

Further evidence supporting the hypothesis that some of the neurons in this region use object-centered descriptions is that their selectivity between the faces of different individuals is maintained across anisomorphic transforms of the stimulus (Hasselmo *et al.*, 1989). However, in most of these cases (16/18 neurons) although the identity of the face was reflected in the neuronal response, viewing angle also influences the response to some extent. It is possible that these latter neurons represent an intermediate stage in the computation of object-centered descriptions.

Also consistent with object-centered encoding is the finding of neurons which respond to images of faces of a given absolute size, irrespective of the retinal image size. These neurons thus show size constancy.

7) Finally, it was shown that the responses of some neurons in this region reflect information about facial expression independently of identity, and that some other neurons reflect information about identity irrespective of facial expression (Hasselmo, Rolls, & Baylis, 1989). This was shown in experiments in which the stimulus set included 3 different expressions of each of 3 different monkeys. Of 45 neurons with responses selective for faces according to the criteria of Baylis, Rolls and Leonard (1985), 9 (20%) showed significant response changes dependent on expression with no effect of identity (compared to 15 which showed an effect of identity independently of expression), as shown by a two-way ANOVA. Examples of the effective expressions were an open-mouthed threat (for 8 neurons in a larger sample) and non-threat expressions (for 8 neurons). These results suggest that there are some neurons in this region the responses of which could be useful in providing information about facial expression, of potential use in social groups. Damage to this population may contribute to the deficits in social and emotional behavior which are part of the Kluver-Bucy syndrome produced by temporal lobe damage in monkeys.

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VISUOMOTOR INTEGRATION

FRED MILES	**"Eye Movement as a Probe for Decoding of Optic Flow by the Primate Visual System"**
ROBERT WURTZ	**"Cortical Control of Pursuit Eye Movements"**
DAVID SPARKS	**"Role of the Superior Colliculus in Sensory-Motor Integration"**

Eye Movement as a Probe for the Decoding of Optic Flow by the Primate Visual System

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Recent experiments on the monkey suggest that there are direct, robust linkages between the visual and oculomotor systems which mediate the ocular following reflex. Normally, this reflex helps to stabilize the moving observer's gaze on objects of interest in the surroundings. When sinewave grating patterns are drifted across the animal's field of view they evoke ocular following responses whose latency is inversely related to--and solely a function of--contrast and temporal frequency, indicating that such responses are merely triggered by local changes in luminance. It has been usual to regard the system exclusively as a visual back-up to the vestibulo-ocular reflex, responding simply to any residual retinal slip during head turns. For this reason the system was assumed to be optimally driven by simple rotational disturbances of the entire retinal image. However, the pattern of optic flow experienced by the moving observer is much more complex than this and includes translational as well as rotational components which result in an uneven flow of images across the retina (motion parallax). Recent experiments indicate than *en masse* movement of the visual scene is not the optimal stimulus for ocular following: the response is better when the motion is restricted to the images in the central retina while the images in the periphery remain stationary. In fact, the response can be improved even further by having the peripheral images move in the opposite direction to those at the center. Such antiphase retinal image motion normally occurs when the moving observer fixates a nearby object: as the eye pursues the images moving across the central retina, the images of the stationary surroundings are swept back across the peripheral retina. Thus, the visual inputs to the ocular following system are so organized that motion parallax helps, rather than hinders, the moving observer's attempts to stablize his/her eyes on nearby stationary objects. In effect, the system performs a dynamic figure/ground discrimination using motion parallax cues. Interestingly, the antiphase pattern of retinal image motion that is optimal for driving ocular following is also a very effective stimulus for some neurons in cortical area MT, a region that others have implicated in visual tracking. These data indicate that ocular following is a visuomotor response that can provide valuable new insights into the nervous system's processing of visual motion information.

Cortical Control of Pursuit Eye Movements

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Cortical area MT is devoted to visual motion processing as indicated by the high proportion of cells that show a directionally selective visual response to moving visual stimuli and as indicated by the deficits in pursuit eye movement and discrimination of visual motion following chemical lesions of this area. MT projects to adjacent regions within the superior temporal sulcus (STS) of the monkey, and neurons in a subregion within this area (MST) also frequently show directionally selective visual responses. In addition, some cells within MST receive an additional extraretinal input during pursuit as indicated by their continuing discharge during pursuit even in the absence of visual motion. These neurons with both visual motion and an extraretinal input are found within two areas within MST. The first is a lateral-anterior area (MSTl) in which many cells respond well to the motion of small spots and which when damaged leads to a deficit in pursuit eye movements. Unlike the retintopic deficit following lesions of extra-foveal MT, deficits following the lesion of MST are directional; pursuit toward the side of the brain with the lesion is reduced regardless of the area of the visual field in which the target starts to move. Electrical stimulation within this area also leads to an acceleration of the eye toward the side stimulated, the inverse of the lesion effect. Because of the nature of the neuronal responses, the lesion deficits, and stimulation effects, this subregion of MST seems highly likely to be related to the generation of pursuit eye movement. Cells in the second region of MST, a region more dorsal and medial in MST (MSTd), more frequently prefer the motion of large visual fields rather than small spots, and are frequently activated by motion in one direction in the central region of the visual field and by motion in the opposite direction by larger stimuli. Lesion or electrical stimulation in this region has only slight effects on the generation of pursuit eye movement, suggesting that the function of this area is other than the generation of pursuit. One possibility is that this region is involved in the distinction of objects that move in relation to a background. Experiments showing that many of these cells show disparity sensitivity with broadly tuned sensitivity for near or far stimuli are consistent with this notion.

The Role of the Superior Colliculus in Sensory-Motor Integration

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Since signals from several sensory modalities converge in the deeper layers of the superior colliculus, a site that also contains cells with motor properties, the superior colliculus may be a brain region where sensory signals are translated into motor commands - commands for orienting the receptors toward the source of significant or novel environmental stimuli. The motor command signal for initiating saccadic eye movements has been studied in most detail. This is a command to correct for motor error (the difference between current and desired eye position) rather than a command to move the eye to a particular position in the orbit. Thus, the task of sensory systems is to specify the change in eye position required to look to a target, not merely the location of the target in head, body or retinal coordinates. This computation requires information about the position of the eyes in the orbits as well as information about the location of the stimulus in space. Experiments will be described indicating that visual and auditory signals found in the deeper layers of the superior colliculus are encoded in motor, rather than sensory, coordinates. The discharge of visual cells is independent of the site of retinal stimulation and the receptive fields of auditory cells shift with changes in eye position. The response of these neurons depends upon motor error rather than the position of the target in space. These findings indicate that it will be fruitful to continue to examine the functional organization of the superior colliculus from a motor perspective. The format of the motor command imposes constraints upon the types of sensory signals that can be used to initiate saccadic eye movements. Rigid requirements are placed upon the transformations that sensory signals must undergo before they are appropriate to guide movements of the eye.

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